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Multi-year data-model evaluation reveals the importance of nutrient availability over climate in arctic ecosystem C dynamics

Efrén López-Blanco¹, Marcin Jackowicz-Korczynski^{1,2}, Mikhail Mastepanov^{1,3}, Kirstine Skov^{1,4}, Andreas Westergaard-Nielsen⁴, Mathew Williams⁵ and Torben R. Christensen¹

¹ Department of Biosciences, Arctic Research Center, Aarhus University, Roskilde, Denmark

² Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

³ Oulanka Research Station, Oulu University, Kuusamo, Finland

⁴ Center for Permafrost (CENPERM), Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark

⁵ School of GeoSciences, University of Edinburgh, Edinburgh, UK

E-mail: elb@bios.au.dk

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Abstract

Arctic tundra is a globally important store for carbon (C). However, there is a lack of reference sites characterising C exchange dynamics across annual cycles. Based on the Greenland Ecosystem Monitoring (GEM) programme, here we present 9-11 years of flux and ecosystem data across the period 2008-2018 from two wetland sites in Greenland: Zackenberg (74°N) and Kobbefjord (64°N). The Zackenberg fen was a strong C sink despite its higher latitude and shorter growing seasons compared to the Kobbefjord fen. On average the ecosystem in Zackenberg took up $\sim 50 \text{ g C m}^{-2} \text{ yr}^{-1}$ (range of $+21$ to $-90 \text{ g C m}^{-2} \text{ yr}^{-1}$), more than twice that of Kobbefjord (mean $\sim 18 \text{ g C m}^{-2} \text{ yr}^{-1}$, and range of $+41$ to $-41 \text{ g C m}^{-2} \text{ yr}^{-1}$). The larger net carbon sequestration in Zackenberg fen was associated with higher leaf nitrogen (71%), leaf area index (140%), and plant quality (i.e. C:N ratio; 36%). Additional evidence from *in-situ* measurements includes 3 times higher levels of dissolved organic carbon in soils and 5 times more available plant nutrients, including dissolved organic nitrogen (N) and nitrates, in Zackenberg. Simulations using the Soil-Plant-Atmosphere (SPA) ecosystem model showed that Zackenberg's stronger CO₂ sink could be related to measured differences in plant nutrients, and their effects on photosynthesis and respiration. The model explained 69% of the variability of net ecosystem exchange of CO₂, 80% for photosynthesis and 71% for respiration over 11 years at Zackenberg, similar to previous results at Kobbefjord (73%, 73%, and 50%, respectively, over 8 years). We conclude that growing season limitations of plant phenology on net C uptake have been more than counterbalanced by the increased leaf nutrient content at the Zackenberg site.

Keywords: Arctic tundra, Greenland, net ecosystem exchange, photosynthesis, ecosystem respiration, nutrient availability

1. Introduction

The Arctic is rapidly changing; ongoing global climate change has already started to redesign high latitude ecosystems and challenge the functioning and resilience of arctic tundra (Box *et al.*, 2019). These high latitude ecosystems contribute to <8 % of the global land area yet they play a key role in the global C cycle (McGuire *et al.*, 2012). Additionally, tundra regions show a marked sensitivity to climatic and environmental changes (ACIA, 2005). Shortening of the spring snow cover duration and increase of vegetation greenness (Myers-Smith *et al.*, 2020) and enhanced permafrost warming (Romanovsky *et al.*, 2017) have serious consequences for ecosystem-atmosphere interactions, and these may result in feedback loops intensifying climate warming further. Thus the response of the terrestrial Arctic C cycle to changes in climate is a major issue of global concern (McGuire *et al.*, 2012). The consequences are, however, broadly uncertain because of past difficulties in conducting research in the Arctic (Metcalf *et al.*, 2018; Virkkala *et al.*, 2019) and its complexity. Despite such challenges there is an urgent need to understand the C cycle sensitivity in high latitudes, reducing model uncertainties (López-Blanco *et al.*, 2019) and identifying the global effects to be able to estimate solid prognostic numbers.

The likely rise in temperature (IPCC, 2013) and precipitation (Bintanja *et al.*, 2020) may have multiple effects on CO₂ exchange, and in turn may initiate a series of critical alterations in ecosystems. Firstly, an increment of photosynthetic C uptake can be driven by lengthening growing seasons, CO₂ fertilisation (Sitch *et al.*, 2008), shrub expansion (Myers-Smith *et al.*, 2011) and vegetation greening (Myneni *et al.*, 1997). Secondly, these increases of C uptake may be counterbalanced by enhanced microbial turnover (Commane *et al.*, 2017), heterotrophic respiration (Webb *et al.*, 2016), methane emissions (Mastepanov *et al.*, 2008; Schuur *et al.*, 2015), grazing and trampling exclusion from large herbivore (Falk *et al.*, 2015), episodic biological events (Lund *et al.*, 2017), and fires (Rocha and Shaver, 2011). Biologically available nutrients in soils, the net result of interacting processes such as precipitation, plant and microbial uptake, and mineralization of organic matter (Rustad *et al.*, 2001), can modify plant growth and turnover rates in arctic tundra nutrient limited ecosystems (Shaver and Chapin III, 1980). Minimal variations in relation to these interrelated processes may lead to changes in ecosystem C sink-source functioning (Williams *et al.*, 2000) and so the full implications of these changes in terrestrial C dynamics remain uncertain (López-Blanco *et al.*, 2019).

The net ecosystem exchange (NEE) of CO₂ is the balance between its two major modulating components: Gross Primary Production (GPP; CO₂ uptake) and Ecosystem Respiration (R_{eco}; CO₂ release). The exchange of CO₂ between terrestrial ecosystems and the atmosphere is a key descriptor of

ecosystem functioning. Eddy covariance (EC) measurements of NEE are a powerful technique for C flux measurements at landscape scale (Baldocchi *et al.*, 2001). Moreover, EC ensures high temporal resolution and minimal disturbance to the surrounding surface and vegetation. However, this method is difficult to implement in northern latitudes due to remoteness and harsh conditions (Lafleur *et al.*, 2012). Factors such as the lack of direct line power and remote connectivity, unavoidable instrument failures, extreme conditions especially in wintertime or the disturbance linked to wildlife, challenge the creation of continuous and robust datasets. Further EC data only measured net fluxes, and so are insufficient to provide a comprehensive and mechanistic picture of the underlying processes driving NEE. Conveniently, process-oriented ecosystem models can represent complex ecosystem processes shaping the NEE of CO₂ (Williams *et al.*, 2000), dynamics of C stocks, and their feedbacks with important arctic related actors such as permafrost (Koven *et al.*, 2015), snow dynamics (Essery, 2015) and vegetation shifts (van der Kolk *et al.*, 2016).

In this study we present a decade of EC data at two contrasting sites, each recorded over consecutive years during 2008-2018 by the Greenland Ecosystem Monitoring programme (GEM; g-e-m.dk) (Christensen *et al.*, 2017). GEM is a state-of-the-art cross-disciplinary research infrastructure leading Greenlandic ecosystem monitoring. We aim in this study to evaluate the drivers of temporal variability and quantify and explain the differences in CO₂ exchange between the northernmost (Zackenberg) and southernmost (Kobbefjord) ecosystem stations. We ask the ecological questions: “How different is high arctic NEE compared to low arctic NEE in Greenland?” and “What are the key driving factors contributing to any identified differences?”. We hypothesize that site-specific differences such as climate, growing season length, and nutrient availability will control the variability of net C uptake between Zackenberg and Kobbefjord. EC measurements of NEE at high temporal resolution are combined with an extensive set of meteorological-, plant phenology- and soil-related observations and process-based modelling to diagnose the key differences of terrestrial net C sink strength in relation with plant phenology timing, leaf nitrogen (N) traits, and organic C and N from soil water. This paper makes use of a rich dataset to establish a robust baseline framework for model calibration and validation and to attribute observed flux differences to key processes.

2. Materials and methods

2.1 Site description

Terrestrial CO₂ exchange measurements have been conducted in Zackenberg fen (Northeast Greenland, 74°N; Figure 1.a) and in Kobbefjord fen (Southwest Greenland,

64°N; Figure 1b) since 2008 under the auspices of the cross-disciplinary GEM programme. These locations characterize high and low arctic sites (Christensen *et al.*, 2017) and are both surrounded by >1000 m.a.s.l mountains and a fjord. Annual mean temperature and precipitation are -8.6°C and 253mm in Zackenberg and 0.3°C and 1081mm in Kobbefjord during the 2008-2018 period. According to the Circumpolar Arctic Vegetation Map (Walker *et al.*, 2005) Zackenberg belongs to the subzone C bioclimate zonation with an average temperature in July of 7-9°C, while Kobbefjord fits the subzone E with an average July temperature of 11-13°C. Both fen sites have water saturated organic soils with an abundant snowmelt water supply. The precipitation falls largely as snow during the shoulder seasons and on average Zackenberg accumulates a slighter thicker (maximum) snowpack compared to Kobbefjord (1 and 0.9 m, respectively). The Zackenberg area has continuous permafrost, with maximum thaw depth variability of 0.5-1m (Lund *et al.*, 2014), whereas no permafrost has been found in Kobbefjord (López-Blanco *et al.*, 2017). The two sites are sedge dominated fens commonly populated with *Eriophorum scheuchzeri* and *Dupontia psilosantha* (Zackenberg) and *Eriophorum angustifolium* and *Scirpus caespitosus* (Kobbefjord) (Bay *et al.*, 2008; Bay, 1998) and an abundant moss layer characterized by the presence of *Sanionia uncinata* and *Sphagnum lindbergii* at each site, respectively (Hassel *et al.*, 2012). The sunlight hours from May to September differ substantially between the two sites, ranging from 14 to 21hrs in Kobbefjord and from 17 to 24hrs in Zackenberg.

2.2 Flux measurements

The EC flux data consist of high temporal resolution measurements for the 2008-2018 period. In Zackenberg the systems consisted of a closed-path infrared gas analyser LI-6262 (LI-COR Inc., USA) and 3-D sonic anemometer Gill R2 (Gill Instruments Ltd, UK) until August 2012, when it was upgraded to an enclosed-path LI-7200 (LI-COR Inc., USA) and Gill HS (Gill Instruments Ltd, UK). In Kobbefjord, the systems have been equipped with a closed-path infrared gas analyser LI-7000 (LI-COR Inc., USA) and a 3-D sonic anemometer Gill R3-50 (Gill Instruments Ltd, UK) until August 2018, when it was upgraded to an enclosed-path LI-7200 (LI-COR Inc., USA). The sonic anemometer in Zackenberg was installed at a height of 3m (and the air intake was attached at the same level) while in Kobbefjord it was at 2.2 m (air intake at 2 m). In both stations we processed the high-frequency CO₂ concentration and wind components data according to standard flux community techniques (i.e. FLUXNET and ICOS), including de-spiking (Højstrup, 1993), 2D coordinate rotation, time lag removal by covariance optimization, block averaging, frequency response correction (Moore, 1986) and Webb-Pearman-Leuning correction (Webb *et al.*, 1980). More information on the EC system setup, flux

computation, and quality checks in Lund *et al.* (2010). We post-processed the quality-checked NEE data using gap-filling and partitioning approaches. On one hand, data-gaps have been filled with a marginal distribution sampling technique (Moffat *et al.*, 2007). On the other hand, the separation of NEE into its two modulating fluxes, GPP and Reco, was achieved via traditional separation algorithms utilized in the FLUXNET community (Reichstein *et al.*, 2005; Reichstein *et al.*, 2016). More information on flux gap-filling using marginal distribution sampling and flux partitioning using ReddyProc (Reichstein *et al.*, 2016) in López-Blanco *et al.* (2017). Due to the absence of true night-time during the growing season in Zackenberg, the data have been processed using the daytime method (Lasslop *et al.*, 2010). The reporting of fluxes in this paper follows the standard micrometeorological sign of convection, i.e. the uptake of carbon (sink) is a negative flux while the release of carbon (source) is a positive flux. Moreover, this study defines the beginning of the growing season as three-consecutive days with negative fluxes (i.e. net C uptake) after the winter period, while the end of the growing season is characterized as three-consecutive days with positive fluxes (i.e. net C release).

2.3 Ancillary measurements

For each site a comprehensive suite of meteorological measurements, phenology related observations, biomass and soil core samples, physical soil parameters, and soil water chemistry have been collected, processed and quality-checked from the GeoBasis and ClimateBasis subprogrammes, all freely accessible from the GEM database (data.g-e-m.dk). The meteorological datasets from nearby climate stations (<2km distance) includes data on air temperature (°C), total precipitation (mm), relative humidity (%), shortwave radiation (W m⁻²), photosynthetic active radiation (W m⁻²), and snow depth (m). The phenology related variables integrate leaf area index (m² m⁻²) at the peak of the growing season and end of the snowmelt period (Day of Year, DOY). Direct harvest measures of leaf area index (LAI) has been calculated using Image J (Schneider *et al.*, 2012) for July 2015 data in Kobbefjord (López-Blanco *et al.*, 2018) and July 2019 data in Zackenberg. The snowmelt period was classified at a pixel level (<20 % snow cover) from a time-lapse camera (HP e427) following the procedures described by Westergaard-Nielsen *et al.* (2017). C and N stocks (leaf, litter, stems, roots, mosses, and soil organic matter; g C m⁻² and g N m⁻²) were collected from 5 plots of 100 cm² area at each fen site following the procedure described in López-Blanco *et al.* (2018). The physical soil parameters integrated in this study contains soil temperature (°C) at different soil depths and snow coverage (%) derived from the time-lapse camera. Soil water chemistry observations include dissolved organic carbon (DOC; ppm), dissolved organic nitrogen (DON; ppm), ammonium (NH₄⁺; ppm), and nitrate (NO₃⁻; ppm) and specific conductivity (EC;

$\mu\text{S cm}^{-1}$). Further details on ancillary measurements from Zackenberg and Kobbefjord can be found in [Lund et al. \(2012\)](#) and [López-Blanco et al. \(2017\)](#).

2.4 Ecosystem modelling focused on arctic processes

We run the Soil-Plant-Atmosphere (SPA) model ([Williams et al., 1996](#); [Williams et al., 2000](#)) with 11 years (2008-2018) of meteorological forcing from Zackenberg, to support previous simulations at Kobbefjord ([López-Blanco et al., 2018](#)). SPA is a mechanistic point model that simulates C, water and energy cycles through eco-physiological principles in a vertically resolved canopy and soil profile. SPA models 1) a radiative transfer scheme differentiating between sunlit and shaded leaf area, 2) photosynthesis based on the classic representation of carboxylation from [Farquhar and von Caemmerer \(1982\)](#) model plus a stomatal conductance model that balances vapour phase losses with hydraulic supply to maximise C uptake, 3) surface energy balance and evaporation based on the Penman-Monteith method, and 4) detailed distribution of water and heat transfer through the soil profile. Furthermore, the model version used here has been refined, calibrated and validated with observational data from Kobbefjord ([López-Blanco et al., 2018](#)), including implementation of important arctic related processes. In this version we 1) independently calculated maintenance respiration losses considering nitrogen (N) interactions based on formulations described by [Reich et al. \(2008\)](#) and not as a fixed ratio, and 2) improved net C uptake timing at the beginning of the growing season by restarting growing degree day summation right after the snowmelt period, using data derived from the *in-situ* cameras ([Westergaard-Nielsen et al., 2017](#)). In [López-Blanco et al. \(2018\)](#) we found that the model's most sensitive parameters to NEE, GPP and R_{eco} were those related to leaf N traits and initial C stocks. Here we followed the approach applied to Kobbefjord data with separate calibration and validation years. Therefore, we manually calibrated the first 5 years of the time series (2008-2012) using the timing of specific snowmelt in Zackenberg to define the start of plant flush, average leaf nitrogen, leaf mass per area (LMA), the maximum foliar C stock (at the peak of the growing season), and the C and N stocks (litter, stem and roots). Finally, the Q_{10} of foliar and root respiration rates has been increased from 2 to 3 at Zackenberg to account for plant thermal acclimation to colder temperatures ([Atkin and Tjoelker, 2003](#); [Tjoelker et al., 2001](#)). The rest of parameters have been kept the same as at Kobbefjord to facilitate a model performance comparison only impacted by the environmental forcing. For validation we calculated linear goodness-of-fit (R^2 and RMSE) of the last 6 years (2013-2018) to evaluate the level of statistical agreement between C flux data (NEE, GPP and R_{eco}) and model simulations.

3. Results

3.1 Interannual variability of meteorological forcing and phenology related variables

Overall, Zackenberg was colder (a difference of -8.9°C) and drier (a difference of 828 mm in precipitation) compared to Kobbefjord. Zackenberg fen, located 10° north of Kobbefjord fen, had lower interannual and interseasonal temperature and precipitation variability between 2008 and 2018 (Figure 1). During this period, annual mean temperatures and total precipitation ranged from -2.4°C to 3.1°C and from 559mm to 1179mm in Kobbefjord, but only between -9.7°C and -6.7°C and 93mm and 436mm in Zackenberg. Kobbefjord featured stronger interannual oscillations (greater than the $-0.3 \pm 2.5^\circ\text{C}$ and $1081 \pm 200\text{mm}$ anomalies delimited by the dotted box in Figure 1b.1) between specific series of years such as 2010 (warmer and wetter), 2011 (colder and drier) and 2012 (warmer and wetter); and 2016 (warmer and drier), 2017 (warmer and wetter) and 2018 (colder and drier). Zackenberg had smaller temperature and precipitation anomalies (not exceeding $\pm 2.5^\circ\text{C}$ and $\pm 200\text{mm}$ Figure 1b.2).

These climatic conditions shaped both the snow regimes and the seasonality of the growing season. First, Zackenberg had 10% greater maximum snow depths in the cold season (October to May) and 23 days delay to the end-of-snowmelt periods than Kobbefjord (Table 1). Second, Zackenberg fen switched from being a source to a sink of CO_2 on July 9th (17 days later than Kobbefjord) and continued with net uptake until August 23rd (5 days before Kobbefjord). Zackenberg fen had an average growing season length of 46 days compared to 66 days in Kobbefjord (Table 1).

3.2 NEE timeseries and cumulative NEE, GPP and R_{eco}

Zackenberg fen had a higher C sink strength ($>170\%$) compared to Kobbefjord fen (Figure 2 and 3) despite its higher latitude and markedly shorter growing season (Table 1 and Figure 2). Zackenberg fen generally acted as a sink of CO_2 over the study period, with an average NEE of $-50 \text{ g C m}^{-2} \text{ yr}^{-1}$ (range $+21$ to $-90 \text{ g C m}^{-2} \text{ yr}^{-1}$), more than twice as strong as Kobbefjord ($-18 \text{ g C m}^{-2} \text{ yr}^{-1}$ with range of $+41$ to $-41 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Figure 3). There were two anomalous C source years, with positive NEE; 2018 in Zackenberg and 2011 in Kobbefjord. Zackenberg 2011 has been associated with an extreme melt season (i.e. one month delay compared to the 2008-2017 period) ([Christensen et al., in review](#)). Kobbefjord featured exceptionally variable meteorology between 2010 and 2011 ([López-Blanco et al., 2017](#)) facilitating optimal conditions for a biological outbreak of the noctuid moth *Eurois occulta* larvae ([Lund et al., 2017](#)) and minimal for plant growth. The NEE of 2011 and 2018 have been ~ 70 and $\sim 83 \text{ g C m}^{-2} \text{ yr}^{-1}$ less productive than the rest of years on average, respectively, and therefore acted as a net source of CO_2 .

In general, the higher C sink strength observed in Zackenberg is linked to larger photosynthesis (i.e. more negative GPP) rather than reduced respiratory losses (i.e. more positive R_{eco}) (Figure 3). Specifically, Zackenberg GPP was on average $-252 \text{ g C m}^{-2} \text{ yr}^{-1}$ (range of -130 to $-317 \text{ g C m}^{-2} \text{ yr}^{-1}$), 18% higher than Kobbefjord GPP ($-213 \text{ g C m}^{-2} \text{ yr}^{-1}$, ranging from $+131$ to $-316 \text{ g C m}^{-2} \text{ yr}^{-1}$). The respiration released from R_{eco} was 7% larger in Kobbefjord ($195 \text{ g C m}^{-2} \text{ yr}^{-1}$, range of 145 to $280 \text{ g C m}^{-2} \text{ yr}^{-1}$) than in Zackenberg ($181 \text{ g C m}^{-2} \text{ yr}^{-1}$, range of 112 to $237 \text{ g C m}^{-2} \text{ yr}^{-1}$).

We found a lower sensitivity to annual air temperature from gross fluxes in Zackenberg (GPP slope = $6.1 \text{ g C m}^{-2} \text{ yr}^{-1} \text{ }^{\circ}\text{C}$ and R_{eco} slope = $1.1 \text{ g C m}^{-2} \text{ yr}^{-1} \text{ }^{\circ}\text{C}$; Figure 4a) compared to Kobbefjord (slope = 32.7 and $25 \text{ g C m}^{-2} \text{ yr}^{-1} \text{ }^{\circ}\text{C}$). This finding is consistent with the lower climate interannual variability revealed in Figure 1 and the smaller sensitivity in growing season length at Zackenberg (Table 1). We found a similar compensatory effect (slope, intercept, R^2 ; Figure 4b) between photosynthesis and respiration both in Zackenberg and Kobbefjord.

3.4 Carbon and nutrient content in vegetation and soils

The enhanced photosynthetic activity (Figure 3 and 4b) has been associated with higher C and N stocks and leaf traits in the aboveground domain and larger concentration levels of nutrients and minerals in soils (Figure 5).

The new *in-situ* information retrieved from the 2019 sampling campaign shows systematic larger C stocks, leaf mass per area (LMA), leaf N, leaf area index (LAI), and plant quality (C:N ratio) in the Zackenberg fen (Figure 5a). The C stocks averaged at the peak of the growing season 74.6 g C m^{-2} in leaves, 106.7 g C m^{-2} in litter, 89.3 g C m^{-2} in stems, and 405.2 g C m^{-2} in mosses. This is 44.7 , 40.4 , 20.1 , and 9.1 more g C m^{-2} in leaves, litter, stems and mosses compared to Kobbefjord C stocks, respectively. Likewise, the leaf trait data pointed to consistently higher leaf N (2.3 vs 1.62 g N m^{-2} leaf area), LMA (58.83 vs 56.29 g m^{-2}), and LAI (1.28 vs 0.52 m^{-2}) in Zackenberg compared to Kobbefjord (Figure 5a). Moreover, we found that the plant quality in Zackenberg fen is 36% higher (i.e. lower C:N ratio) than Kobbefjord fen (Figure 5a).

The water chemistry data from the first 50cm of Zackenberg fen topsoil show consistent higher levels of Dissolved Organic C (DOC), Dissolved Organic N (DON), nitrates (NO_3^-), ammonium (NH_4^+), and electroconductivity (EC) during the 2015-2017 period (Figure 5b). Overall, the belowground domain had 3 times more DOC (ppm), 5 times more nutrients such as DON (ppm) and NO_3^- (ppm), 2 times more K^+ (ppm), and 5 times higher EC ($\mu\text{S cm}^{-2}$), and slightly more acidic pH (Figure 5b) in Zackenberg. Likewise, alkaline cations (Ca^{2+} and Mg^{2+}) are 13 and 5 times higher while the acidic cations (Mn^{2+} and Fe^{2+}) are 21 and 7 times higher in Zackenberg fen (Figure S1).

3.5 Calibration and validation of the process-based model

The SPA model can realistically characterise 11 years of data from the Zackenberg fen (Figure 6) and 8 years of data from Kobbefjord (see López-Blanco *et al.* (2018)), with model setup varying according to *in-situ* biomass and tissue N data. At Zackenberg the daily aggregated NEE ($R^2 = 0.69$; RMSE = $0.4 \text{ g C m}^{-2} \text{ d}^{-1}$), GPP ($R^2 = 0.80$; RMSE = $0.5 \text{ g C m}^{-2} \text{ d}^{-1}$) and R_{eco} ($R^2 = 0.71$; RMSE = $0.6 \text{ g C m}^{-2} \text{ d}^{-1}$) matched the independent summertime field observations for the validation period (2013-2018). The snowmelt period information retrieved from the photo monitoring, has been used to restart the growing degree day summation, modelling the NPP allocation into the different C pools. This implementation improved significantly the beginning of the growing season timing ($R^2 = 0.92$) and only resulted in an average 4-day shift compared to the SPA calculation.

The SPA modelling showed that the observed difference in plant tissue N concentrations at Zackenberg relative to Kobbefjord could explain the identified increase the C uptake at the high Arctic site indicated by the EC observations (Figure S2). SPA can generate a system consistent with Zackenberg fluxes only by parameterisation based on the biomass sampling data from the field campaign (average leaf N, LMA, maximum foliar C stock, initial C stocks of litter, roots and stems and C:N ratio in roots; see section 3.4). Using the initial calibration from Kobbefjord under Zackenberg climate fails to simulate annually aggregated NEE within the observation's range (Figure S2). However, once the new information on C and N is updated in SPA, together with the updated Q_{10} of foliar and root respiration rates, the yearly aggregated NEE mean for the Zackenberg site between 2008 and 2018 is $-54.9 \pm 50.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ while the NEE value extracted from the EC tower is $-54.9 \pm 20.9 \text{ g C m}^{-2} \text{ yr}^{-1}$. This finding shows the importance of the C and N changes, and emphasises the importance of N to C fluxes.

4. Discussion

4.1 How different is high arctic NEE compared to low arctic NEE in Greenland?

Zackenberg fen features lower interannual climate variability with systematically colder and drier conditions (Figure 1), thicker snowpack, later snowmelt period (Table 1), and shorter periods with net photosynthetic uptake during growing seasons compared to Kobbefjord fen (Table 1, Figure 2). These meteorology- and phenology-related conditions have not been an obstacle to greater C uptake than Kobbefjord, on average 32 g C m^{-2} more (Figure 3), despite the shorter growing seasons. In this study longer growing seasons are not necessarily translated into larger net C uptake, similar to previous findings from Lund *et al.* (2010) and Parmentier *et*

al. (2011). On average Zackenberg sequesters more C ($NEE = -70.8 \text{ g C m}^{-2} \text{ yr}^{-1}$) than other arctic wetlands at lower latitudes reported by Coffey and Hestir (2019) (Table S1; mean $NEE = -47.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ and range of -119 to $+79.3 \text{ g C m}^{-2} \text{ yr}^{-1}$) during the same period (June 1st to August 31st). Moreover, we found at least three specific extreme events that have notably disturbed the growing season C budget at both Zackenberg and Kobbefjord (Figure 3). On one hand, a natural larvae outbreak had a significant impact on vegetation productivity in 2011 in Kobbefjord (Dahl et al., 2017; Lund et al., 2017). López-Blanco et al. (2017) estimated a shift from source to sink of $-30 \text{ g C m}^{-2} \text{ yr}^{-1}$ as average for the 2008-15 period to a source of $41 \text{ g C m}^{-2} \text{ yr}^{-1}$ while Lund et al. (2017) reported a counterbalanced increase of C sink strength through the following 3 years. On the other hand, Christensen et al. (in review) have reported multiple ecosystem effects triggered by extreme meteorological conditions indicating 1) a decrease of $18\text{--}23 \text{ g C m}^{-2} \text{ yr}^{-1}$ (close-to-zero NEE) during a 9-day rain event in 2015 and 2) a 314% weaker C sink strength in 2018 compared to the 2008-17 period forced by an extraordinary late snowmelt (i.e. 1 month delay in maximum daily CO_2 uptake and 20 days shorter growing season). Reductions of $20\text{--}40 \text{ g C m}^{-2} \text{ yr}^{-1}$ are not trivial as these are similar to typical arctic fen ecosystem annual C budgets (Parmentier et al., 2011).

Zackenberg fluxes were less sensitive to temperature compared to Kobbefjord (slopes of the regressions from Figure 4a), perhaps linked to reduced phenological variability at this site (Table 1). This study also found a compensatory effect between photosynthesis (GPP) and respiratory losses (R_{eco}) for both sites (Figure 4b) similar to previous findings reported in López-Blanco et al. (2017) and previously described by Richardson et al. (2007) and Wohlfahrt et al. (2008). We noted however that the overall contribution to NEE in Zackenberg was dominated by photosynthesis ($39 \text{ g C m}^{-2} \text{ yr}^{-1}$ more than Kobbefjord) compared to respiration ($14 \text{ g C m}^{-2} \text{ yr}^{-1}$ less) (Figure 3 and 4b). Consequently, controls of photosynthesis will be given a higher priority in the following sections.

4.2 What are the key driving factors contributing to the identified differences?

Our results suggest that the limitations of plant phenology timing and colder temperatures in Zackenberg regarding net C uptake have been more than counterbalanced by the increased content of plant tissue N, linked to richer soil nutrients. Here, it is the difference in nutrient availability, not the difference in climate, that explains the divergence in net C uptake between the two sites (Figure 3, 4, 5, and S2). But at each site climate governs the interannual variability. We found higher N concentration levels in above- and below-ground plant tissues and soil water. It is well-known that arctic tundra ecosystems are generally nutrient limited (Chapin III and Shaver, 1985)

and that soil nutrient availability shape the patterns of plant abundance (Shaver and Chapin III, 1980). Yet, site-specific differences such as geology, climate boundary conditions, flora, and fauna will control differences in nutrient availability between Zackenberg and Kobbefjord, which again contributes to differences in net C uptake.

4.2.1 C and N content in the aboveground domain

The average foliar N measured in Zackenberg (2.76 g N m^{-2}) is substantially larger compared to Kobbefjord (1.61 g N m^{-2} ; López-Blanco et al. (2018)) (Figure 5). Our foliar N estimate is similar to values previously described in the Zackenberg fen system; for instance Arndal et al. (2009) reported 2.25 g N m^{-2} in 2004 during the peak of the season, Street et al. (2012) presented 2.57 g N m^{-2} in 2006 and Mosbacher et al. (2019) quantified 2.0 g N m^{-2} in 2015. Interestingly, Arndal et al. (2009) found that the Zackenberg fen was the most productive system in terms of photosynthesis despite presenting the lowest biomass compared to the four surrounding ecotypes (mostly heathlands), featuring the highest leaf N, leaf chlorophyll, and moss content per unit ground area. These authors also proposed that a higher C sink strength is likely controlled by the N content in photosynthesizing tissues. Plants with high leaf N will have an enhanced productivity in fens (Aerts and Chapin, 1999; Chapin III, 1980). Our *in-situ* data (Figure 5) suggest that plant C uptake is highly dependent on nutrient and mineral availability, and this explains differences in fluxes between Zackenberg and Kobbefjord (Figure S2). This result opposes those from Siberian tundra sites, where microbes depolymerized, mineralized and immobilized N amounts more than the maximum capacity for plant N uptake (Wild et al., 2018).

Additionally, Street et al. (2012) found evidence that the well documented positive relationship between foliar N and LAI (Williams and Rastetter, 1999; van Wijk et al., 2005) is not shifted towards lower foliar N at high latitudes. In fact, the observed values of top canopy N per unit area were highest at Zackenberg, the second most northerly site among other low and high arctic sites such as Toolik, Barrow, Abisko and Svalbard. The authors also tested the hypothesis that lower irradiance at higher latitudes may modify the optimal development of leaf area with respect to available N; they have not found a direct result of changes in latitude and therefore day-length and/or sun angle. This finding is in line with our results (see Figure S3) using a random forest machine-learning technique (López-Blanco et al., 2017; Pedregosa et al., 2011); the importance of photosynthetic active radiation to NEE at diurnal, seasonal and annual scales in Zackenberg (with 24-h daylight in the arctic summer) was not larger than in Kobbefjord. Likewise, Street et al. (2012) found a significant correlation between the LAI-leaf N curvature and diffuse fraction of total shortwave radiation. The differences in diffuse radiation seems to be explained by cloud frequency,

and Zackenberg had the lowest average summer diffuse fraction compared to Toolik, Barrow, Abisko and Svalbard. The fact that Zackenberg has lower precipitations and higher air pressure suggest less cloud cover and thus lower summer diffuse fraction compared to Kobbefjord (data not shown). This finding is important because under diffuse conditions N is distributed more uniformly due to greater light penetration (Roderick *et al.*, 2001; Meir *et al.*, 2002), regardless of other important factors such as canopy height, leaf angle and geometry (Street *et al.*, 2012).

Grazing patterns have in recent years been identified as a major driving factor for vegetation dynamics and in turn greenhouse gas exchanges in northern wetlands. Recent studies have demonstrated that small and large herbivory exclusion is capable of altering the CO₂ balance and CH₄ emissions (Falk *et al.*, 2015), being able to switch even the typical C sink during peak growing season into a source (Lara *et al.*, 2017). Moreover, the presence of muskox in Zackenberg has been associated with significant increases of N concentration and enhanced plant quality (i.e. C:N ratio) (Mosbacher *et al.*, 2019). Such changes are typically observed in experiments when herbivores are removed from the system (Johnson *et al.*, 2011; Henry *et al.*, 1990). The C:N ratio reported in this study from Zackenberg (21.7) is systemically lower (i.e. higher plant quality) than Kobbefjord (33.8) (López-Blanco *et al.*, 2018) and is within the range of previous observations retrieved from the same location: 22.9 (Arndal *et al.*, 2009), 21 (Mosbacher *et al.*, 2019), and 16.7 (Street *et al.*, 2012).

Higher C uptake capacity may also be positively influenced by the large abundance of mosses (405 g C m⁻²) and the high moss N content (10 g N m⁻²) (Arndal *et al.*, 2009; Street *et al.*, 2013). Bryophytes are well adapted to low light, unlike vascular plants that have a low light compensation and saturation point (Glime, 2007). Hence mosses, and not the graminoids, could be an important cause of enhanced C sink in moss-dominated high arctic ecosystems during the shoulder seasons when the leaf area is reduced. In this study we show that the Zackenberg fen mosses are the major contributor to aboveground dry biomass and the total C and N pool, agreeing with previous findings from Falk *et al.* (2015) and Arndal *et al.* (2009). This, together with N₂-fixing cyanobacteria closely associated with mosses benefiting from water saturated conditions, can enhance productivity in photosynthetic active tissues. Likewise, more moss biomass may contribute indirectly to higher C uptake (enhanced GPP) and N leaf pool sizes as the moss layer facilitate the cyanobacteria to reach larger biomass than on bare soil, thus enhancing N fixation and N availability (Arndal *et al.*, 2009).

4.2.2 C and N content in the belowground domain

Our results show a higher availability of DOC and nutrients (DON, NO₃⁻, NH₄⁺, K⁺) for plant and microbial uptake in soils

from Zackenberg during the 3-year overlap of available data (Figures 5). Likewise, we found higher values of electroconductivity, commonly associated to a high presence of both cations (K⁺, Ca²⁺, Mg²⁺, Al³⁺, Mn²⁺, and Fe²⁺) and anions (Cl⁻, NO₃²⁻, SO₄²⁻, HCO₃⁻). In water saturated environments such as Zackenberg and Kobbefjord, nutrient concentrations are likely determined by the extensive lateral transport from adjacent slopes (Rasmussen *et al.*, 2020). Giblin *et al.* (1991) concluded that *in-situ* mineralization rates of a tundra site in Alaska could not explain the available N by itself, indicating a lateral transport of nutrients into the system from the surrounding areas. The catchment for Kobbefjord fen is dominated by slow-weathering Precambrian gneisses (Søndergaard *et al.*, 2012), releasing very few (nutritive) minerals, as opposed to the catchment for Zackenberg fen with a high abundance of faster-weathering basalts and sedimentary deposits (Cable *et al.*, 2018). The downslope hydrological transport of mineral-rich weathered material is consequently higher in the Zackenberg fen catchment. Moreover, the available ions in the upper soil layers is likely elevated across the Zackenberg area due to an overall negative water balance (Westergaard-Nielsen *et al.*, 2020), whilst a positive water balance in the Kobbefjord area will favour higher levels of ion leaching from the upper soil.

During the snowmelt period in spring both Zackenberg and Kobbefjord meltwater redistributes N from uphill areas down to the low-lying fen areas. During snowmelt, the soil is still frozen, so a majority of the meltwater (and thus the soluble ions) will probably run-off as a pulse on the surface to the rivers in the first week of snowmelt (Westergaard-Nielsen *et al.*, 2019). In Zackenberg though, the fen is located in a wider catchment basin, which may favour higher landscape retention of the snowmelt water compared to Kobbefjord. Also, the possible slowing of run-off meltwater by richer biomass and larger flat areas may facilitate the accumulation of nutrients, explaining the high C and N pool sizes found in the soil water chemistry data. High values of DON, and especially oligopeptides (Farrell *et al.*, 2013), sustain faster plant and microorganism growth than does dissolved inorganic N during very short growing seasons, indicating plant adaptation to arctic ecosystems (Näsholm *et al.*, 1998). On top of that, changes in the active layer depth can result in substantial ecological and terrain disturbances such as soil organic C and N availability. For example, the existence of continuous permafrost in Zackenberg may help to retain N availability better than permafrost-free areas such as Kobbefjord (Olefeldt *et al.*, 2014; Harms and Jones Jr., 2012). Likewise, the uppermost part of the permafrost soil can immediately release more nutrients and plant-available N than active layer soils (Reyes and Loughheed, 2015; Keuper *et al.*, 2012). These findings suggest that nutrients from the active layer could resupply and enrich the water column with ions from thawing

permafrost, releasing a significant amount of plant-available N and ultimately stimulating net primary production.

4.3 What can be learnt from process-based ecosystem modelling?

Our CO₂ exchange estimations for the 2008-2018 snow-free period using local meteorological forcing at Zackenberg and Kobbefjord can explain a significant part of the high temporal variability in NEE, GPP and R_{eco} (Figure 6, [López-Blanco et al. \(2018\)](#)). In order to achieve the model calibration we relied primarily on *in-situ* data collected in 2019 during the monitoring field campaign. This aboveground biomass and soil core sampling effort was purposely designed to fill C cycle model calibration knowledge gaps. In [López-Blanco et al. \(2018\)](#) we highlighted two important messages from Kobbefjord - N-related plant traits are the most sensitive parameters in the SPA model and therefore field data on C:N ratios decrease the model uncertainty. At Zackenberg, datasets on snowmelt period, leaf N, leaf mass per area, C:N ratio of roots, and C stocks of leaf, litter, stem, roots were critical to match model simulations with local observations of NEE (Figure S2). The SPA model confirms that the differences in C cycling between the two sites are best explained when information about site-specific leaf nutrient parameters is included in the model. There is ample evidence from field manipulations of the sensitivity of primary production to nutrient additions at high latitudes, mediated by changes in plant traits ([Shaver et al., 2001](#)). Our results support other Arctic biogeochemical modelling studies, e.g. TEM ([McGuire et al., 1992](#); [Zhuang et al., 2003](#)) and MEL ([Rastetter and Shaver, 1992](#); [Rastetter et al., 2013](#)), which concluded that regulation of arctic C cycling at the landscape and regional scales was linked to nutrient controls via C/N/P stoichiometry of plant tissues.

We also increased Q₁₀ of foliar and root respiration rates to improve the plant respiration sensitivity to temperature since Zackenberg is ~8.3°C colder on annual basis (Figure 1). [Atkin and Tjoelker \(2003\)](#) have shown that Q₁₀ is not constant as it increases near-linearly with decreasing temperatures; short-term increases in temperature can have a greater potential impact on plant respiration in plants growing in cold climates (with an average leaf respiration Q₁₀ ~ 2.5-3). Likewise, [Heskel et al. \(2014\)](#) revealed how in Toolik lake Q₁₀ values also decreased with temperatures from ~3.0 at 5°C to ~1.5 at 35°C. In this version of SPA ([López-Blanco et al., 2018](#)), maintenance respiration is calculated based on a modified version of the [Reich et al. \(2008\)](#) equation built from on a strong respiration-nitrogen relationship. The fact that SPA shows a better agreement with EC observations with higher Q₁₀ (Figure S2) suggests that plants are thermally acclimated to colder temperatures and that respiration triples (i.e. Q₁₀ = 3.0), and not doubles, per 10°C rise in temperature ([Atkin and Tjoelker, 2003](#)) at this high Arctic site.

In this study we show how to parameterize the SPA model with *in-situ* data from a single year peak season (Figure 5 and S2). However, higher temporal information on C and N pool variability, similar to [Arndal et al. \(2009\)](#) or [Mosbacher et al. \(2019\)](#), may help understand the underlying processes and responses in shoulder season dynamics such as the snowmelt period, the rapid green-up and green-down phases and even extreme events such as a moth outbreak. Additionally, single year data may introduce bias. For example, 2019 (when the *in-situ* samples were collected) was an unusual warmer summer with thinner snow coverage compared to the 2008-2018 trend, and thus this year's meteorology may have enriched the allocation of biomass more than previous years. However, as noted earlier, our N samples in foliage in 2019 were close to values measured in other years. Finally, in relation with the model performance, the effect of changes in precipitation may have a role of interannual variation in fluxes. We found that the coefficient of determination for modelled vs measured NEE during anomalously dry summers was reduced (0.55) compared to wet summers (0.78) at Zackenberg. Further investigations of carbon-water interactions are required.

Using a simple set of parameters we can model high resolution temporal CO₂ exchange with a good degree of agreement in complex arctic tundra ecosystems of varying fertility, climate and meteorology. We believe this modelling framework forms an ideal framework for analysing new sites. Model simulations compared with results from multiyear CO₂ exchange measurements can identify key process uncertainties, feedbacks between structure and function, and the sensitivity to extreme conditions. Two components are required to establish a description of the basic ecosystem-atmosphere interactions in the absence of direct flux measurements: 1) a quantification of the basic biomass and soil core sampling considering C and N status of the ecosystem, and 2) an ecosystem modelling component, e.g. SPA, describing the basic C dynamics based on key driving parameters, and linking C and N in plant tissues, independent of measured fluxes. Ecosystem modelling frameworks can fill process-based knowledge gaps, investigate climate feedbacks, and generate prognostic scenarios exploring the likely future implications of climate change on arctic tundra C cycle dynamics.

5. Conclusions

In this paper we used 20 years of EC measurements to explore CO₂ exchange from two twin ecosystem stations in Greenland, Zackenberg (74°N) and Kobbefjord (64°N). Based on our findings we concluded that:

1. Zackenberg fen has a significant higher C sink strength during repeatedly shorter growing seasons compared to Kobbefjord fen.

2.
- Zackenberg is a nutrient richer fen - the increased C uptake strength is associated with 1) systematic higher C and N stocks, plant traits and enhanced plant quality in the aboveground domain, and 2) higher levels in soils of DOC, nutrients such as DON, NO₃⁻, NH₄⁺, K⁺, and electroconductivity in the belowground domain.
3.
- We conclude that, despite the shorter growing season, carbon uptake and exchanges at Zackenberg were larger due to more nutrient rich plant tissues.
4.
- More sites for high-temporal monitoring of terrestrial C dynamics are needed, especially in sensitive and rapidly changing arctic ecosystems, to establish robust baselines for model calibration and validation, thereby underpinning ecological forecasting techniques.

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Data availability statement

Observational data from the Greenland Ecosystem Monitoring (GEM) programme are freely available from the GEM database (data.g-e-m.dk). Post-processed data and scripts are available from the corresponding author upon reasonable request.

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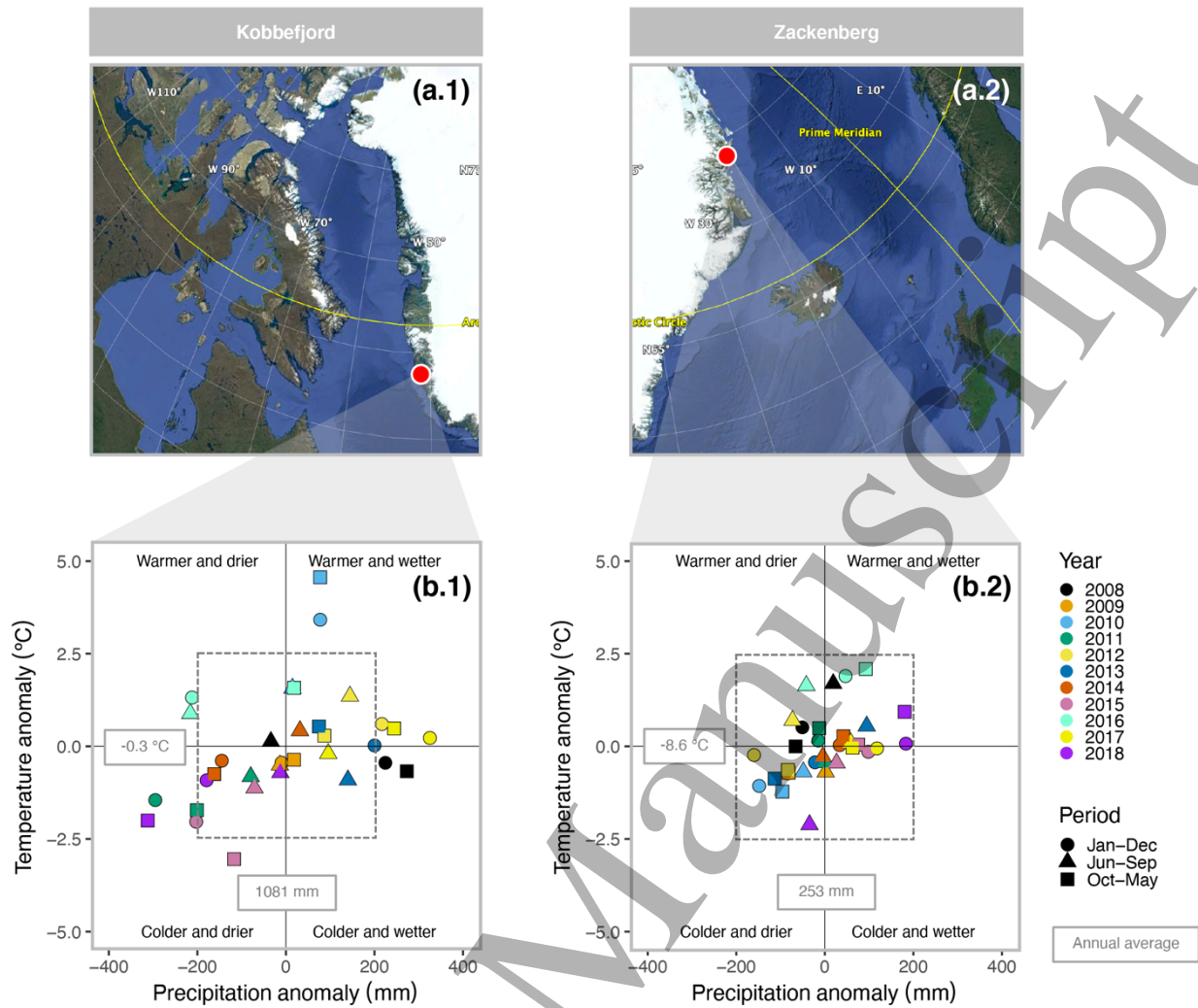


Figure 1. (a.1 and a.2) Location of the Nuuk-Kobbefjord and Zackenberg sites, respectively (source: Google Earth Pro). **(b.1 and b.2)** Annual temperature and precipitation anomalies within the analysed years (2008–2018) including annual (January to December), warm season (July to September) and cold season (October to May) averages.

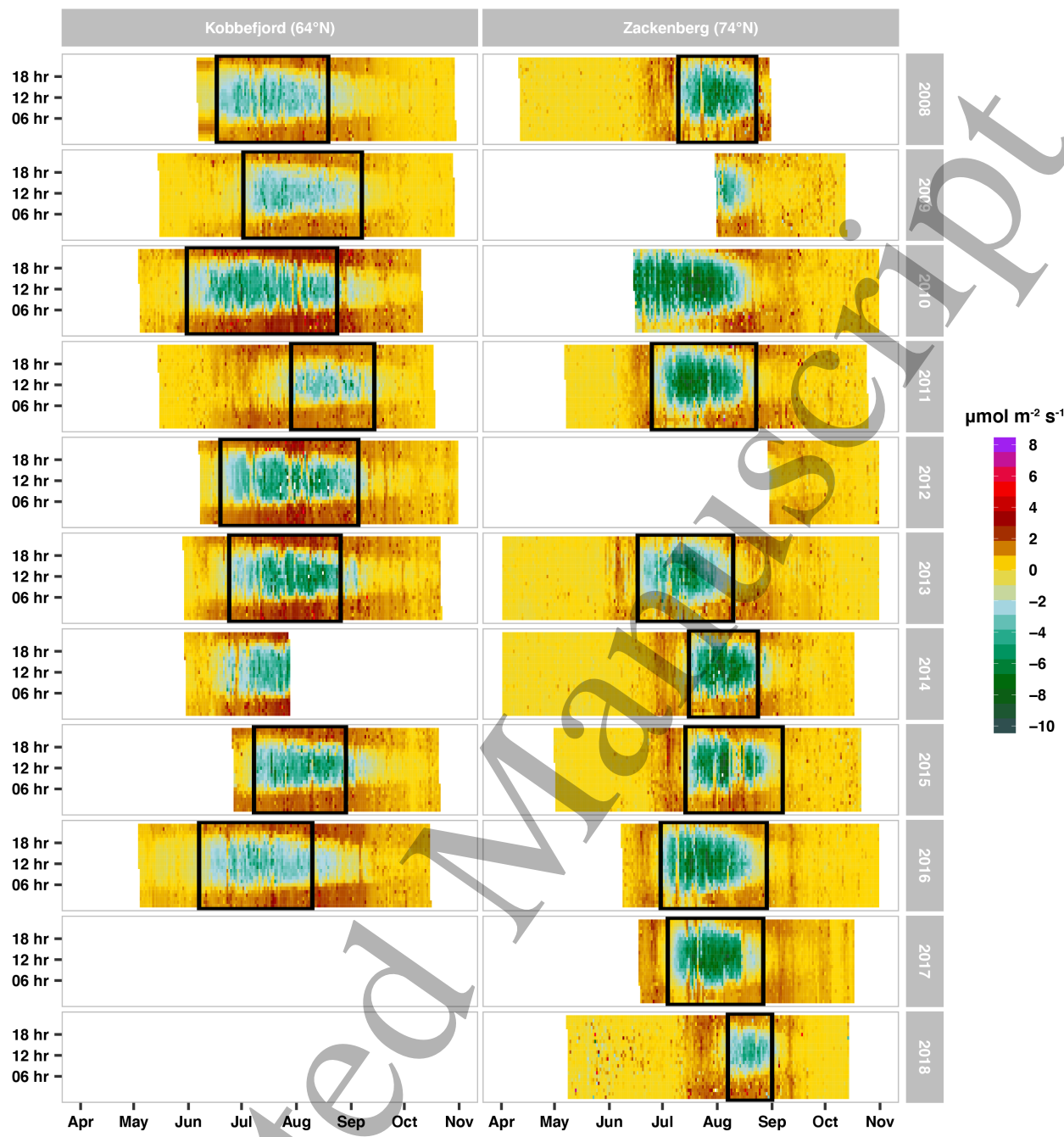


Figure 2. Time series of gap-filled NEE (2008-2018) based on the MDS algorithm from REdyProc. Green represents C uptake while the orange-dark-red denotes C release. The black box delimits the period between the start and the end of the growing season.

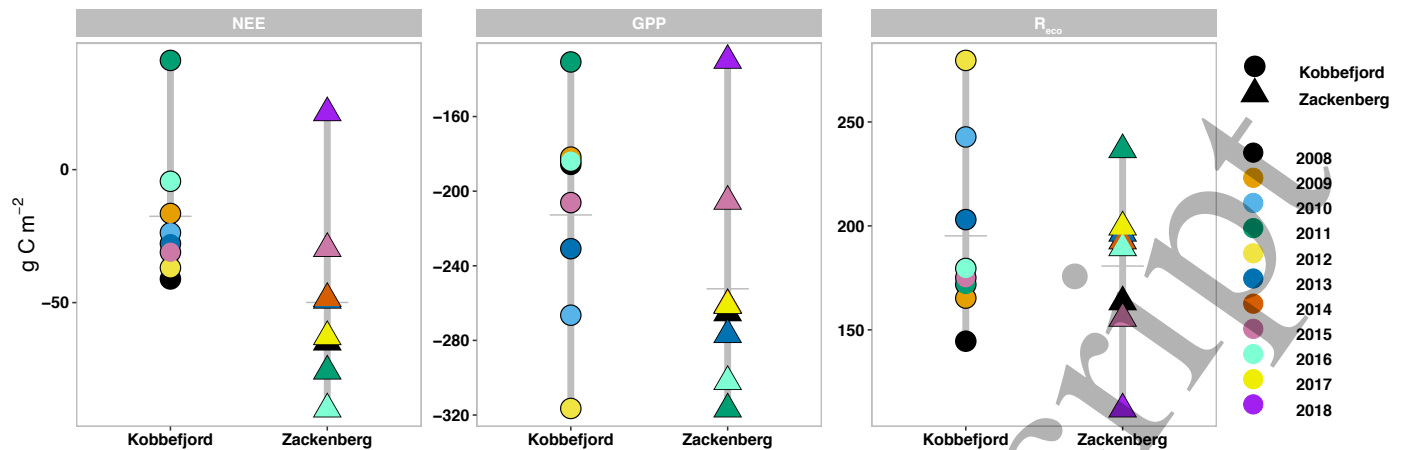


Figure 3. Cumulative ranges (vertical grey bar) and mean (horizontal grey bar) for NEE, GPP and R_{eco} from 2008 through 2018 in Kobbefjord (circles) and Zackenberg (triangles). Years with more than half growing season missing data have been omitted in this calculation.

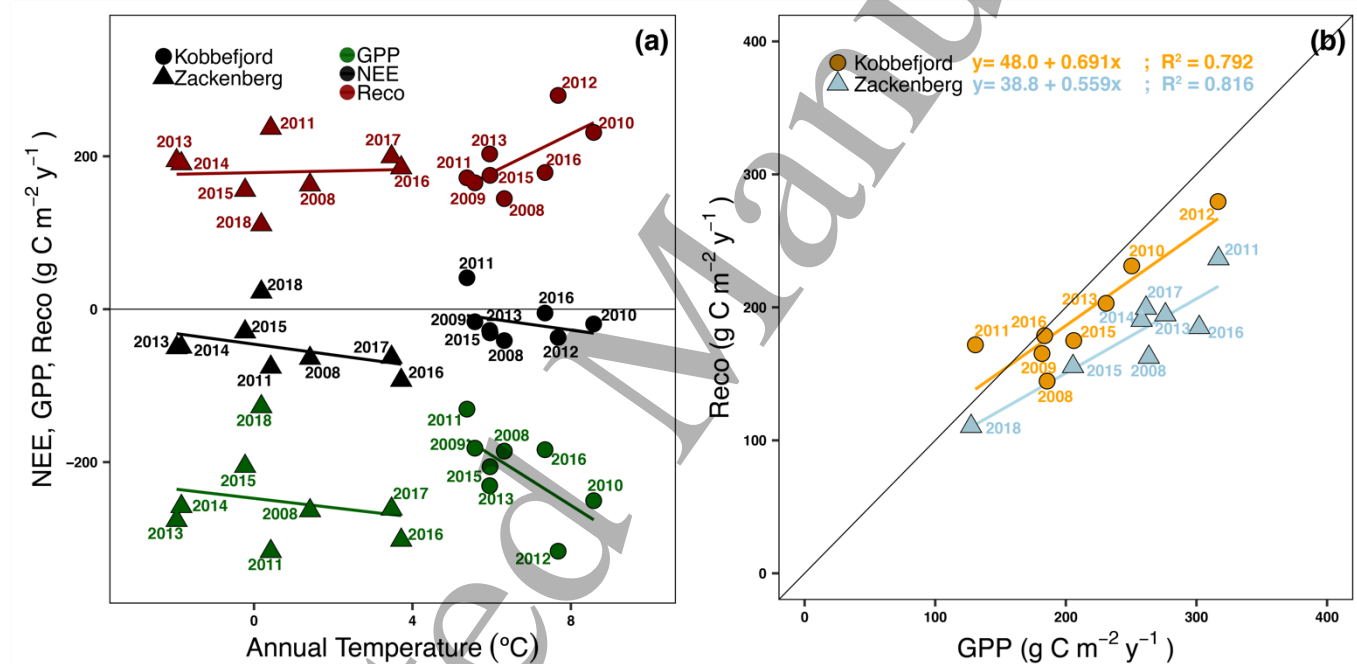


Figure 4. (a) The relationships between observed NEE (black), GPP (dark green), R_{eco} (dark red) ($\text{g C m}^{-2} \text{ year}^{-1}$) and mean temperature ($^{\circ}\text{C}$) between May and October for the years 2008–2018. (b) Interannual variability between GPP and R_{eco} relationships in Zackenberg (light blue) and Kobbefjord (orange). Years with more than half growing season missing data have been omitted in this calculation.

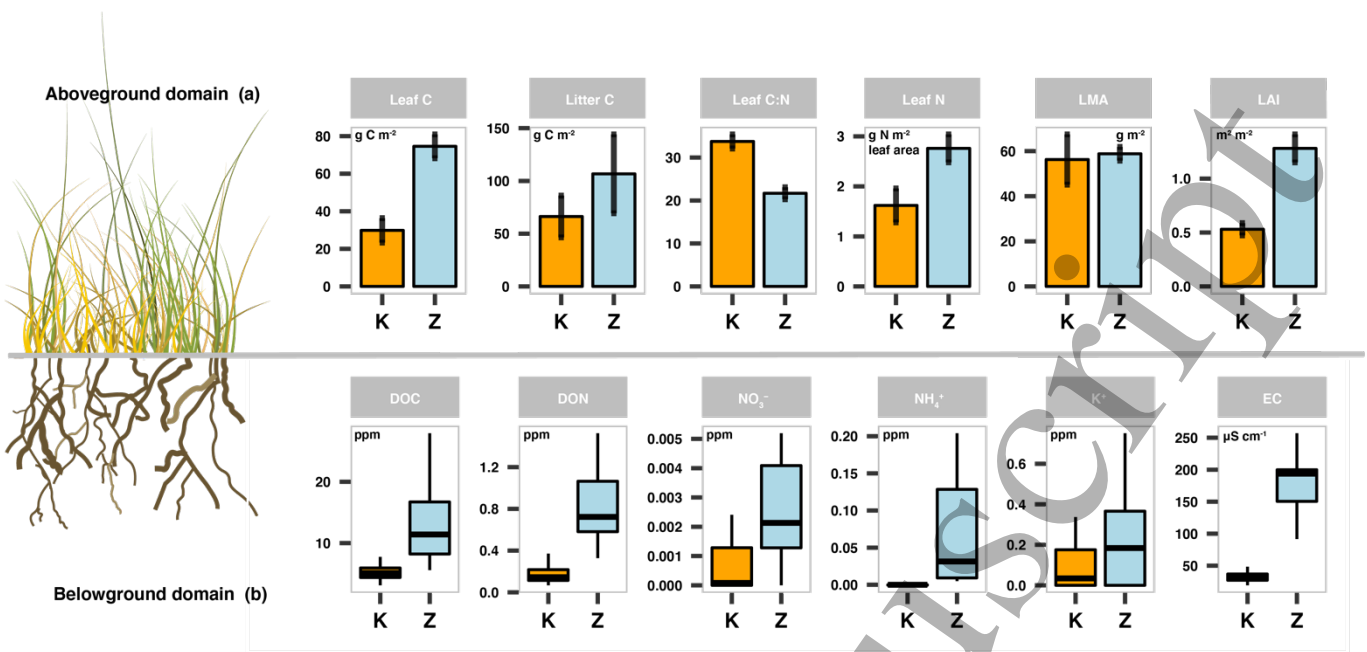


Figure 5. *In-situ* observations from aboveground biomass (a) and concentration levels of nutrients and minerals in soils (b) from Zackenberg fen (light blue) and Kobbefjord fen (orange). The bar plots characterize leaf and litter C stocks, leaf C:N ratio (i.e. plant quality), leaf N, leaf mass per area (LMA), and leaf area index (LAI) in the aboveground domain. The error bars contain the variability (standard deviation) out of the 5 fen plots. The box plots characterize soil water chemistry and catchment exports of dissolved organic carbon (DOC), dissolved organic nitrogen (DON), nitrate (NO_3^-), ammonium (NH_4^+), potassium (K^+), and electroconductivity (EC) between 2015 and 2017 at maximum depth of 50 cm.

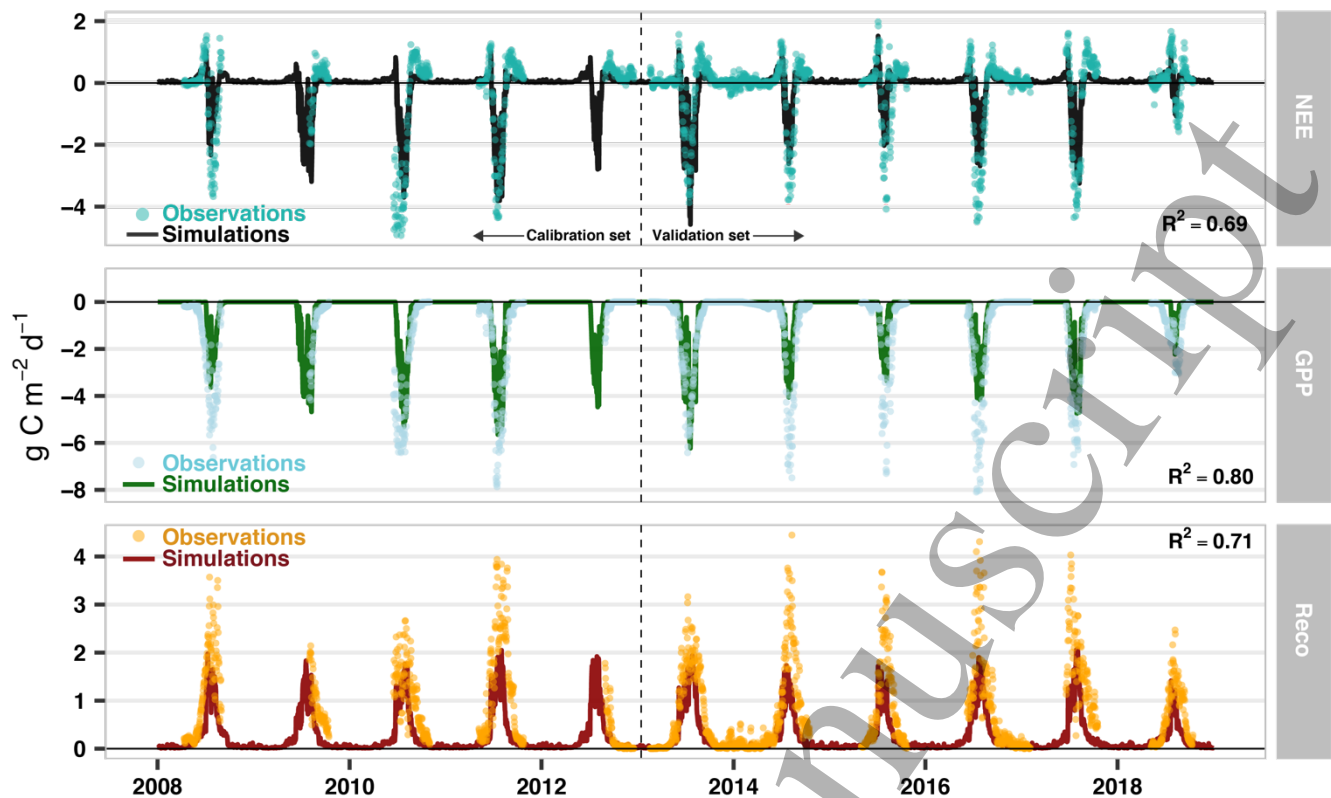


Figure 6. Time series of observed and simulated C fluxes (NEE, GPP, and R_{eco}) using the Soil-Plant-Atmosphere (SPA) model in the Zackenberg site for the 2008-2018 period. The model uses the parameterization calibrated for Kobbefjord data (López-Blanco *et al.*, 2018) including modifications of the initial C stocks, leaf N, leaf mass per area (all based on *in-situ* field data), and Q_{10} of foliar and root respiration rates. Goodness-of-fit (R^2) are only displayed for the validation period (2013-2018).

Table 1. Summary of phenology-related variables in Kobbefjord and Zackenberg for the 2008-2018 period. Grey boxes in the background represents years where full set of variables are complete.

Site	Variable (unit)	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	Average
Kobbefjord	Maximum snow depth (m)	0.6	1	0.3	1.4	1	0.6	1.1	1.2	0.5	1.3	1.1	0.9
	End of snowmelt period (DOY)	148	159	125	165	152	158	156	176	122	156	170	153
	Beginning of growing season (DOY)	167	182	150	209	169	174	169	188	151	-	-	173
	End of growing season (DOY)	230	249	235	256	247	237	-	246	221	-	-	240
	Length of growing season (DOY)	63	67	85	47	78	63	-	58	70	-	-	66
Zackenberg	Maximum snow depth (m)	1.3	0.4	0.7	0.6	1.3	0.5	0.9	1.4	1.1	0.9	1.4	1.0
	End of snowmelt period (DOY)	184	156	174	171	183	155	182	184	169	171	202	176
	Beginning of growing season (DOY)	191	-	-	177	-	168	197	198	180	186	219	190
	End of growing season (DOY)	236	229	229	228	-	222	242	246	234	235	244	235
	Length of growing season (DOY)	45	-	-	51	-	54	45	48	54	49	25	46